The Use of Infauna by Juvenile *Penaeus aztecus* Ives and *Penaeus setiferus* (Linnaeus)

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ABSTRACT: *Penaeus aztecus* Ives, the brown shrimp, and *Penaeus setiferus* (Linnaeus), the white shrimp, co-occur in Texas salt marshes as juveniles. Although their life cycles are similar, evidence indicates that the species utilize different resources for the primary faunal element of their diets. Prey selection and growth studies have shown that brown shrimp successfully remove infauna from natural sediment. Further, a diet of polychaetes, whether alone or in combination with algae, produced growth in the species. Brown shrimp appear to be trophically linked to infaunal populations, thus the structure and dynamics of the benthic community may directly affect local brown shrimp productivity. Areas dominated by surface-dwelling polychaetes as opposed to deep burrowers may provide more accessible foraging opportunities for juvenile brown shrimp. By contrast, white shrimp neither removed infauna nor grew to a significant degree when provided polychaetes or amphipods as food. White shrimp are omnivorous but do not rely on infaunal material to the same extent as brown shrimp. The primary faunal element in the diet of white shrimp has not yet been identified. The dietary differences between the two species may play a role in determining which species dominates in regions with varying marsh accessibility. Although not the only factors influencing penaeid survival and growth, prey choice and availability may greatly affect production and local success of penaeid populations.

Introduction

Salt marshes along the northern Gulf of Mexico serve as one of the primary nursery habitats for juvenile white shrimp (*Penaeus setiferus* (Linnaeus)) and brown shrimp (*Penaeus aztecus* Ives) (Zimmerman and Minello 1984). Marshes provide young penaeid shrimp refuge, reducing levels of predation (Minello and Zimmerman 1983; Minello et al. 1989). The role of marsh habitat as feeding grounds for shrimp, another component of the nursery function (Minello and Zimmerman 1983; Minello et al. 1989), is not yet clear as little is known of the natural dietary habits of penaeid shrimp.

Although *Penaeus* species exhibit the same overall life cycle, brown shrimp are an early spring arrival, first appearing as postlarvae in marshes from late February to early April. White shrimp, however, do not immigrate into marshes until late May or June (Pearson 1939; Williams 1955; Baxter and

Renfro 1966; Farfante 1969; Copeland and Bechtel 1974; Williams 1984).

Salt marshes change in several ways during the interval between these successive peaks in penaeid immigration. Benthic infauna and epifauna reach their maximum seasonal abundance during early spring (March) and decline rapidly after the arrival of seasonal predators (Coull and Palmer 1984; Coull 1985; Flint and Kalke 1985; Zimmerman et al. 1990). Edaphic algae, by contrast, may be available for consumption regardless of the month (Pomeroy 1959; Gallagher 1971; Sullivan and Moncreiff 1987). Further, marsh habitat tends to be warmer, with higher salinities and lower water levels in summer compared with the spring.

Once the shrimp have reached the estuarine areas of the upper Texas coast, the spatial distribution patterns of the two penaeid species differ. Brown shrimp are seasonally attracted to the marsh surface, occurring there in higher densities than in open water areas from late March to November. During the winter months, brown shrimp are present in very low numbers and are equally distrib-

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uted between the marsh surface and the adjacent unvegetated subtidal bottom. White shrimp, by contrast, are often not significantly different in density between the marsh surface and adjacent subtidal bottom during their residence period (Zimmerman and Minello 1984; Zimmerman et al. 1984; Minello and Zimmerman 1985). These spatial patterns may indicate potential dietary differences between the species.

Postlarval and juvenile brown shrimp are omnivorous (Jones 1973; Gleason and Wellington 1988). They are known to consume animals in situ and grow when fed laboratory diets that include animal material (Zein-Eldin 1963; Shewbart et al. 1973; Hunter and Feller 1987; McTigue and Zimmerman 1991). Growth success from consumption of plants depends on the species consumed (Cook and Murphy 1969; Gleason and Zimmerman 1984; Gleason 1986; Gleason and Wellington 1988). Gleason and Zimmerman (1984) found that of all the plant-based diets provided, postlarval brown shrimp grew more rapidly when fed the diatom *Skeletonema*. Diatoms may be an important vegetal food source for the animals (Gleason 1986). This may be because chains of diatoms can settle onto surfaces and may be more readily obtained by the penaeid. Brown shrimp can survive when fed plant-based diets, but the resultant rate of growth was at maintenance levels only (Zein-Eldin 1963; Gleason and Zimmerman 1984).

The white shrimp, also considered an omnivore (Weymouth et al. 1933; Broad 1965), was previously thought to be a more selective feeder than brown shrimp (Karim 1970; Lindner and Cook 1970). Animal protein is consumed by and supports growth of white shrimp (Hunter and Feller 1987; McTigue and Zimmerman 1991). The gut contents of juvenile white shrimp usually contain unrecognizable matter, but remains of polychaetes, tanaids, copepods, foraminifera, ostracods, and fish have been positively identified (Williams 1955; Mayer 1985). In sediment from a South Carolina estuary, white shrimp did not deplete the total number of macroinfauna, nor *Streblospio benedicti* specifically, but a decrease in *Capitella* abundances was observed (Service et al. 1992). This conflicts with the results of gut content analysis to a certain degree but may be an indication of the low relative importance of infauna in this penaeid's diet. White shrimp have been shown to feed on plants in nature (Hunter 1984). In laboratory studies, most plant-based diets produced little or no growth in this species, with the sole exception of *Skeletonema*. When McTigue and Zimmerman (1991) fed this species of diatom to white shrimp, the shrimp grew at a rate, up to Day 20 of the experiment, that was not significantly different from growth resulting

from an animal-based diet. By Day 24, though, the *Skeletonema*-fed shrimp all died, while the animal-diet group survived (McTigue and Zimmerman 1991).

Both brown shrimp and white shrimp demonstrated increased growth when fed combination animal and plant diets over animal or plant diets alone (McTigue and Zimmerman 1991). There is evidence suggesting a difference in the extent to which the two species utilize potential plant and animal resources. Brown shrimp grow significantly more in length and weight when fed an animal diet than do the white shrimp. When plant material was added, both species grew at increased rates that were not significantly different from one another (McTigue and Zimmerman 1991). The plant material may be of greater significance in the diet of the white shrimp than in the brown shrimp. Preliminary research suggests that differences such as this in feeding between the shrimp species may be linked to variations in the life cycles of the animals (McTigue and Zimmerman 1991).

Brown and white shrimp have been classified as bottom feeders who consume any available organic material (Williams 1955; Young 1959; Darnell 1961). Further research, however, indicated that both penaeids are more selective feeders than previously thought (Karim 1970; Condrey et al. 1972; Gleason and Zimmerman 1984). Shrimp walk along surfaces, probing and handling items they encounter (Dall et al. 1990). Frequently, this material is brought to the shrimp's mouthparts and some species such as the pink shrimp (*Penaeus duorarum*) are known to consume infauna (Nelson and Capone 1990). It seems reasonable to suggest that prey available from the substrate, such as benthic invertebrates, could constitute an element of the diets of brown shrimp and white shrimp. The relative importance of such prey items may vary with the species of shrimp, however.

The purpose of this study was to examine similarities and differences in feeding preferences of white shrimp and brown shrimp with reference to naturally occurring prey in estuarine systems. Earlier studies involving the consumption of animal-based diets by shrimp have utilized prey such as *Artemia*, which do not coexist with the shrimp in nature. In the research presented here, we compared and contrasted dietary linkages between each of the penaeid species and the dominant infaunal groups present in Texas salt marshes. The objectives of this project were to determine if brown shrimp and white shrimp can successfully remove infauna from natural sediment and if the penaeids grow when utilizing such resources.

The temporal and spatial separation of brown shrimp and white shrimp in nature may indicate

food resource partitioning. A comparison of the feeding habits of these penaeids may help to define their role in Texas salt marsh communities.

Methods

INFAUNAL REMOVAL EXPERIMENT

Cores of sediment (10 cm diameter, 8 cm depth) without vegetation were collected from the surface of a salt marsh in Galveston Island State Park in sections of PVC pipe. The salt marsh in this area is highly reticulated and is dominated by *Spartina alterniflora*. Sediments consist of fine-grained muds, with little sand or shell material. The cores were carried in 18.93 l (5 gal) buckets to the National Marine Fisheries Service's Galveston Laboratory. The 20-cm sections of PVC pipe that surrounded and supported each core had two mesh (500 μm) inserts opposite of each other, reaching from just above the sediment surface to the top edge of the pipe. These microcosms were held four per bucket and maintained in a temperature-controlled water bath (25°C) with a fixed photoperiod (12 h of light). Temperature and photoperiod were standardized across the experiments to minimize the effects these variables might have on the shrimp and the potential prey organisms. Light was provided by four fluorescent bulbs suspended approximately 1 m above the experimental area. Aerated seawater was added to each bucket to bring the water level up to 8 cm above the sediment surface of the cores. The seawater was continually aerated throughout each experiment.

Juvenile shrimp were captured by seine from the same marsh. Each animal was weighed and introduced into a core, which was then covered with plastic film to prevent the escape of the animal. Control cores were covered as well to provide consistent treatment. After 4 d, the shrimp were removed, weighed, and preserved. Sediment from the cores was sieved through 500 μm mesh and infaunal organisms were preserved for later enumeration and identification. Control cores, free of shrimp, were maintained side-by-side with treatment cores. Both treatment and control groups consisted of at least eight replicate sediment cores. This procedure was repeated twice using brown shrimp (February 23, 1990, mean initial shrimp weight = 0.0132 g, SE = 0.0012; May 31, 1990, mean initial shrimp weight = 0.0954 g, SE = 0.00855) and twice using white shrimp (August 10, 1990, mean initial shrimp weight = 0.0284 g, SE = 0.0055; October 29, 1990, mean initial shrimp weight = 0.2091 g, SE = 0.0156). The first experiments coincided with initial immigration of the species (early season) and the second experiments were near the end of the residence period (late season). Data from sieved cores that inadvertently contained potential competitors (grass shrimp, fiddler crabs, and other penaeids) of the experimental shrimp were not included in the analysis. A comparison of the effects of shrimp on infaunal abundance was made for each penaeid species during both early and late residence periods.

T-tests were used for each of the four experimental dates to determine differences between treatment and control cores for the overall abundance of infauna. A multivariate analysis of variance (MANOVA) was used on log +1 transformed data for each shrimp species. Each of the most abundant infauna species or taxonomic groups were used as dependent variables. Differences between treatment and control cores and early and late season were considered, as was the interaction between these effects. The multivariate F-statistic corresponds to the Wilks' lambda statistic.

GROWTH EXPERIMENT

To determine differences in growth response between the two penaeids to naturally available foods, the following categories were chosen: amphipods alone, polychaetes alone, the diatom *Skeletonema costatum* alone, amphipods plus *Skeletonema*, or polychaetes plus *Skeletonema*. These categories represent major potential food sources occurring naturally in salt marshes. Previous experimentation indicated that *Skeletonema* produced more growth in juvenile shrimp than other algae tested (Gleason and Zimmerman 1984; McTigue and Zimmerman 1991). Species of polychaetes and amphipods were provided in the same relative proportions in which they were collected from the field. Although the abundances of the various species available day-to-day in the field changed, their relative proportions remained fairly consistent throughout the growth study.

Shrimp were held in aerated, filtered seawater (300 ml) in individual 800-ml beakers at 25°C with 12 h of light per day. Mean (±1 SE) initial weights were 0.1333 g ± 0.0044 and 0.0769 g ± 0.0032 for brown shrimp and white shrimp, respectively. Both species of shrimp were fed material from each of the above food categories as treatments, and starved controls were maintained. Each treatment and control group consisted of 20 penaeids. Growth over a period of 30 d was determined as well as the amount of animal material consumed. Food was provided daily ad lib, with both weight and number of prey organisms recorded. Size ranges of prey were randomly mixed. The diatom *Skeletonema* was grown in the laboratory using F2 medium (Guillard 1975). The cultures were centrifuged to separate algal cells from culture media. The *Skeletonema* was then resuspended in filtered

TABLE 1. A) Results of *t*-tests comparing total numbers of infaunal abundances between control cores of sediment and those in which brown shrimp had fed for 4 d (both early and late in the shrimp's residence period). B) MANOVA using the Wilks' Lambda statistic to test for effects of the presence of a brown shrimp on the abundance of the dominant infaunal taxa found in the cores of sediment. The abundance values were log +1 transformed before being used as dependent variables. The variable date includes data from early and late in the shrimp's residence period and the treatments were the presence or absence of a brown shrimp.

A.		Total Infaunal Abundance		
		T	d.f.	p-Value
February 23, 1990		4.3009	14	0.0007
May 31, 1990		2.3697	11	0.0373

B.		Multivariate			
	Value	F-Value	Num d.f.	Den d.f.	p-Value
Date	0.081	22.753	12	24	0.0001
Treatment	0.238	6.395	12	24	0.0001
Date × treatment	0.647	1.089	12	24	0.4109

Univariate (p-values)
Polychaetes

Annelids	d.f.	*Streblospio benedicti*	*Melinna maculata*	*Leitoscoloplos fragilis*	*Heteromastus filiformis*	*Capitella capitata*	Oligochaetes
Date	1	0.0464	0.0001	0.0001	0.0142	0.3528	0.7401
Treatment	1	0.0004	0.9056	0.1282	0.1885	0.5594	0.0242
Date × treatment	1	0.9190	0.0239	0.1282	0.1292	0.4291	0.2289
Residual	35						

Amphipods

Arthropods	d.f.	*Ampelisca abdita*	*Corophium louisianum*	*Grandiderella bonneroides*	*Edotea* sp.	*Hargeria rapax*	Chironomid
Date	1	0.0001	0.0001	0.0182	0.0392	0.0512	0.0001
Treatment	1	0.0029	0.0067	0.3545	0.1227	0.0002	0.0022
Date × treatment	1	0.0925	0.2840	0.5292	0.2133	0.1944	0.0066
Residual	35						

(0.5 μm), natural seawater and provided to the shrimp in beakers at a density of 5×10^5 cells ml^{-1}. Cell counts were monitored daily and the beakers were enriched to maintain constant cell count, if needed. Every 5 d the water in the beakers was changed, the penaeids were weighed individually, and their incremental growth calculated.

The number of days each shrimp survived was analyzed and diets and species of the shrimp were compared using analysis of variance (ANOVA). The data were log transformed to take into account heterogeneity of variances between treatments. When significant interactions between diet and shrimp species were indicated (p-value ≤ 0.05), a priori contrasts were used to determined relationships between the factors.

The change in weight over 5-d intervals was used as a measure of growth rate. Interval weight changes up to day 20 for shrimp consuming amphipods, polychaetes, amphipods plus *Skeletonema*, and polychaetes plus *Skeletonema* were analyzed using a repeated measures ANOVA. This statistical procedure takes into account the relatedness of growth data from one interval to another. Only data up to day 20 were used to ensure adequate sample sizes for the four treatment diets. Significant interactions between the species of shrimp

and among diets were analyzed with a priori contrasts to further delineate differences.

Results

INFAUNAL REMOVAL EXPERIMENT

Brown shrimp significantly reduced the total number of infaunal organisms in the sediment cores during each experiment (Table 1 and Fig. 1). Of the most abundant infaunal worms (Table 1 and Fig. 2), brown shrimp reduced the densities of *Streblospio benedicti*, *Melinna maculata*, and oligochaetes. *Streblospio* was found at significantly different densities during the two experimental runs and were found in significantly different abundances in the treatment and control cores. *Melinna maculata* exhibited a significant interaction between date and treatment. This polychaete was reduced in abundance in the presence of the shrimp during the early experimental run, when the worm was relatively common. During the late experimental run, however, when abundances were lower, the density of *Melinna* was actually slightly higher in the cores that contained a shrimp. Oligochaetes were not found in significantly different densities between the two experimental runs but were significantly lower in the treatment as compared to the control cores. All crustaceans considered were
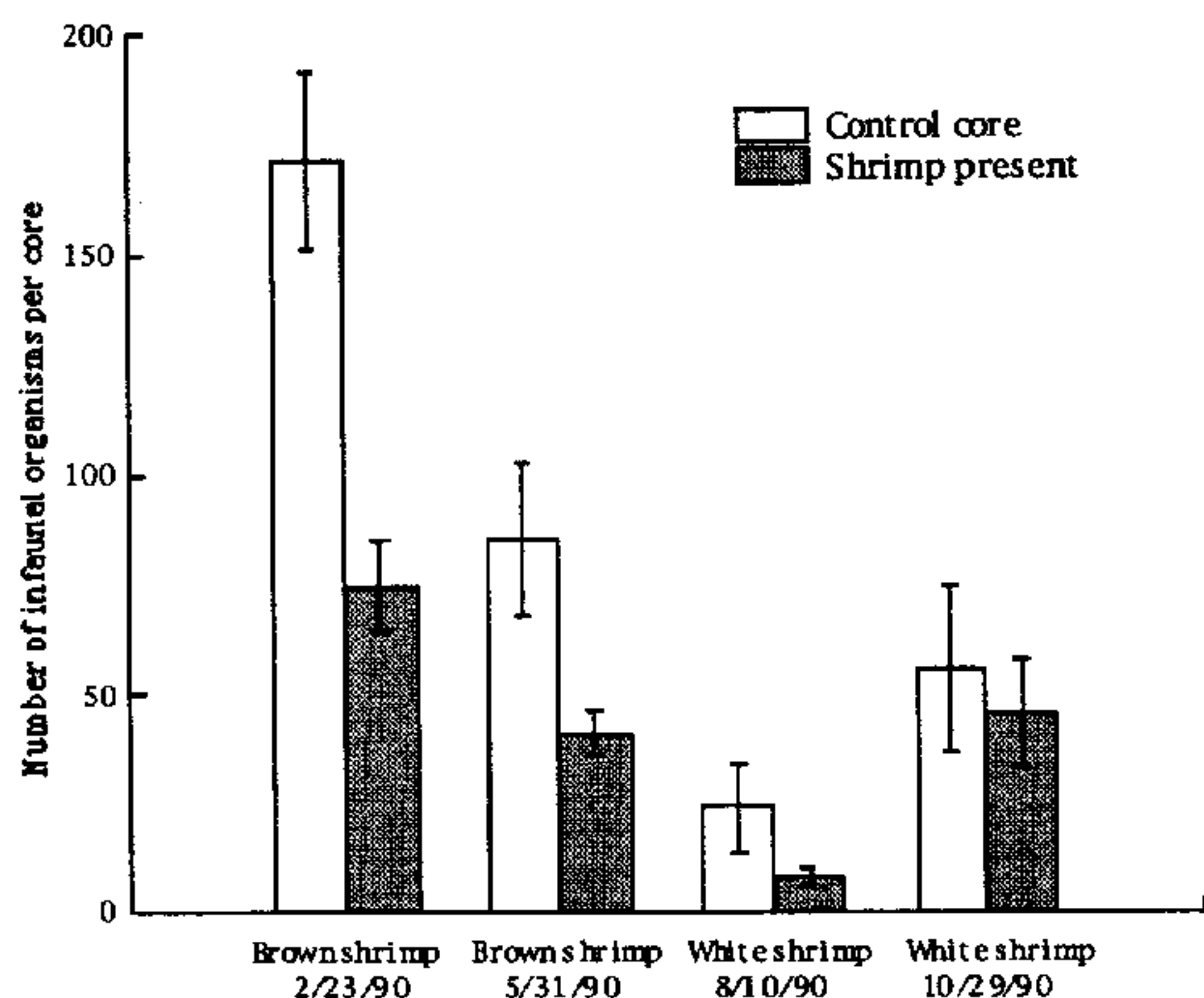
Fig. 1.   A comparison of infaunal densities between control cores and cores in which penaeid shrimp had fed for 4 d. The species of shrimp and date of initiation of the experiment are noted below the bars. Error bars indicate one standard error. Each core had a surface area of 78.54 cm² and a depth of 8 cm.

less abundant during the May experimental run as compared to the February one. *Ampelisca abdita, Corophium louisianum,* and *Hargeria rapax* were significantly reduced in abundance when a brown shrimp was present in the core as compared to the control cores. *Edotea* (an isopod) and *Grandiderella bonneroides* (an amphipod) were not found to be significantly influenced in density by the presence of a brown shrimp. Chironomid larvae were reduced in treatment cores as opposed to control cores, but this difference was not consistent between experimental runs as very few chironomids were present during May.

White shrimp did not significantly affect the overall abundance of infauna in the cores. Neither the main effects of date or treatment nor their interaction were significant in the multivariate analysis (Table 2 and Fig. 3).

A comparison of growth between species over the 4-d period of exposure to the sediment cores indicated that brown shrimp grew consistently more than white shrimp (Fig. 4). This was evident in both early and late trials.

GROWTH EXPERIMENT

During the 30-d growth experiments, survival of brown shrimp and white shrimp fed similar diets was significantly different (Table 3 and Fig. 5). When the experimental diets included polychaetes (both polychaetes alone or in combination with *Skeletonema*), survival of both species was not significantly different but brown shrimp lived longer

overall. White shrimp survival was significantly less than that of brown shrimp on all other diets.

The combination animal-plant diets increased the survival in both species as compared to *Skeletonema* alone (Table 4). Conversely, the addition of algae did not significantly affect the survival of brown shrimp, regardless of the type of animal material offered. White shrimp did not show a difference in survival between the amphipod and amphipod plus *Skeletonema* treatments, although they lived longer on a polychaete diet compared to a polychaete plus *Skeletonema* diet. White shrimp were able to survive significantly longer on polychaete-based and combination plant-animal diets than on all others. Brown shrimp showed no difference in growth between the two polychaete-based diets, although combination diets prolonged survival.

When incremental growth was considered, species × diet and time × diet interactions were significant for the overall model (Table 5). Within each 5-d increment of time, the species × diet interaction was consistently significant (Table 6).

When contrasts were constructed using the species × diet interaction term for the entire model, patterns became evident both between and within species. Brown shrimp consistently grew more quickly than white shrimp (Table 7 and Figs. 6 and 7). Further, brown shrimp consistently had a greater weight change than white shrimp when both species were fed polychaete-based diets or those consisting of animal material alone. Comparative growth patterns resulting from amphipod-based diets and those containing both plant and animal material were not consistent. During some intervals significant differences were evident, whereas in others there were no differences.

The combination of algae and animal food did not consistently increase the growth rate of brown shrimp (Table 7 and Fig. 8). Polychaetes, though, without fail increased brown shrimp growth rates over diets that included amphipods. This remained true regardless of the presence of diatoms.

White shrimp did not show any differences in growth between polychaete and polychaete + *Skeletonema* diets (Table 7 and Fig. 9), nor was there a significant difference between the animal-plant combination diets. Shrimp fed amphipods did not differ consistently in their growth rate from shrimp fed either amphipod + *Skeletonema* or polychaetes alone. The wet weight of both polychaetes and amphipods consumed during a 5-d period was calculated for shrimp in the combination animal-vegetal treatments (Fig. 10). Brown shrimp consumed greater biomass of polychaetes and amphipods per time interval than did white shrimp. Both species
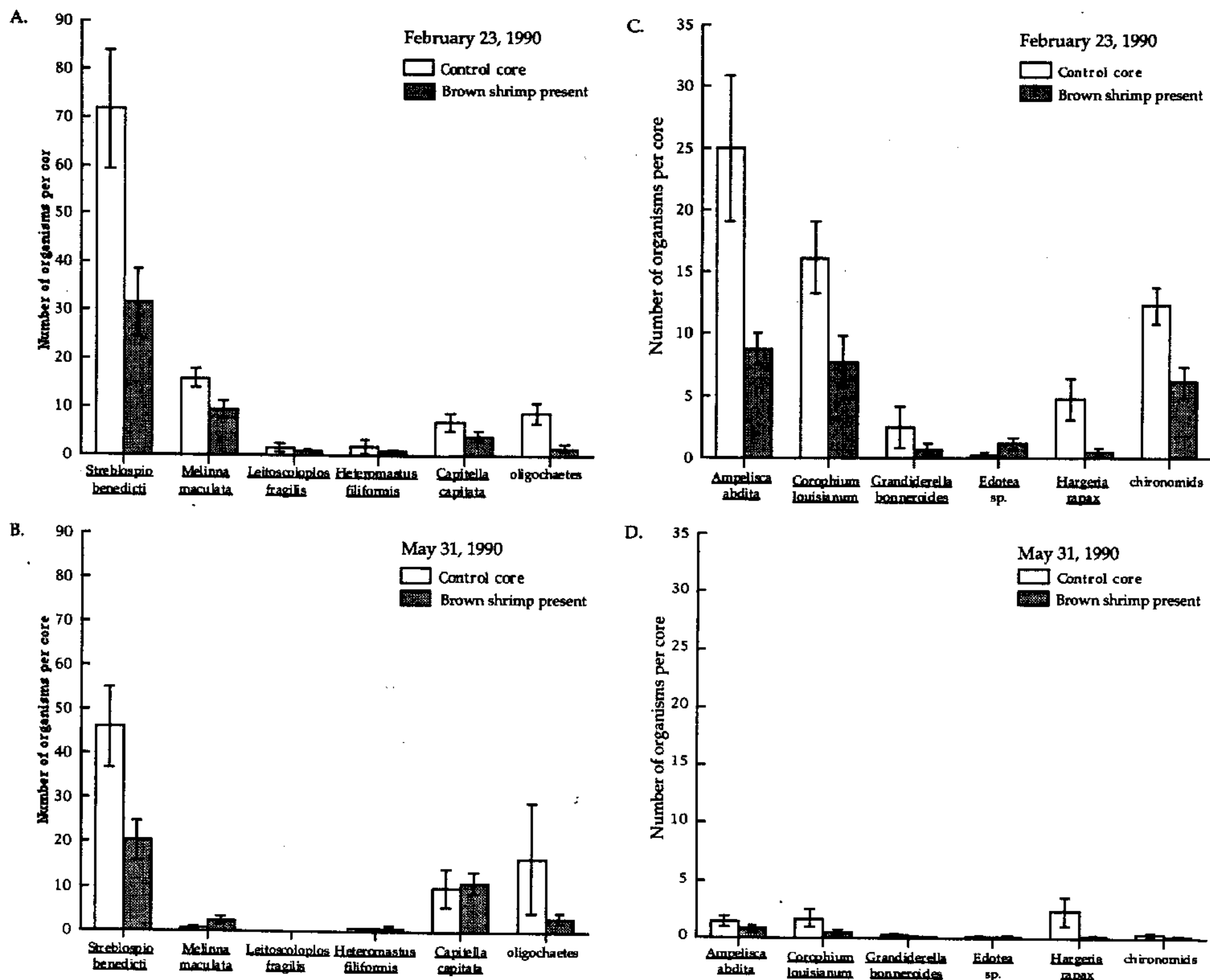
Fig. 2. Depletion of abundant infaunal taxa in cores (78.54 cm²) in which brown shrimp were held for 4 d. Error bars indicate one standard error. (A) Results for annelid taxa during the early season experiment beginning February 23, 1990. (B) Results for annelid taxa during the late season experiment beginning May 31, 1990. (C) Results for arthropod taxa during the early season experiment beginning February 23, 1990. (D) Results for arthropod taxa during the late season experiment, beginning May 31, 1990.

consumed a greater wet weight of polychaetes than amphipods.

Discussion

There is evidence to indicate possible dietary differences between juvenile brown shrimp and white shrimp. While their basic life cycles are similar, brown shrimp occur at times and places in Texas estuaries that coincide with higher abundances of infauna, particularly polychaetes. Brown shrimp enter marsh areas in the early spring when infaunal populations are frequently at their yearly peak. During the first weeks of the brown shrimp's residence in the early spring, there is often no significant difference in their distribution between the intertidal marsh surface and nonvegetated subtidal open water areas (Zimmerman and Minello 1984; Zimmerman et al. 1984; Minello and Zimmerman

1985). Importantly, it is during the early spring season that there is the least difference in infaunal densities between the two habitats. As the season progresses and infaunal levels in open water areas decline relative to the marsh, brown shrimp are found more frequently on the marsh surface with its higher abundance of worms. By contrast, white shrimp immigrate into bays during the summer when infauna are already reduced and these shrimp often distribute without regard to marsh or open water habitat.

Brown shrimp and white shrimp differed in their ability to remove infauna from sediment (Fig. 1). During both early and late season experiments, brown shrimp significantly reduced the abundance of superficial burrowing polychaetes, such as spionids (Table 1; D. Harper personal communication; see Fauchald and Jumars 1979 for review).

TABLE 2. A) Results of t-tests comparing total numbers of infaunal abundances between control cores of sediment and those in which white shrimp had fed for 4 d (both early and late in the shrimp's residence period). B) MANOVA using the Wilks' Lambda statistic to test for effects of the presence of a white shrimp on the abundance of dominant infaunal taxa found in the cores of sediment. The abundance values were log +1 transformed before being used as dependent variables. The variable date includes data from early and late in the shrimp's residence period and the treatments were the presence or absence of a white shrimp.

A.	Total Infaunal Abundance				
	T	d.f.	p-Value		
August 10, 1990	1.5240	10	0.1585		
October 29, 1990	0.4333	10	0.6740		

B.	Multivariate (Wilks' Lambda)				
	Value	F-Value	Num d.f.	Den d.f.	p-Value
Date	0.571	2.408	5	16	0.0826
Treatment	0.713	1.289	5	16	0.3167
Date × treatment	0.726	1.209	5	16	0.3491

		Univariate (p-values) Polychaetes				Amphipods
	d.f.	Streblospio benedicti	Neanthes succinea	Capitella capitata	Oligochaetes	Corophium louisianum
Date	1	0.0088	0.7788	0.8240	0.0319	0.0001
Treatment	1	0.6351	0.2248	0.1693	0.0200	0.0067
Date × treatment	1	0.2096	0.7382	0.9108	0.2534	0.2840
Residual	20					

The removal of tubiculous crustaceans from the sediment was statistically significant during both early and late seasons for brown shrimp (Table 1 and Fig. 2). During corresponding experiments using white shrimp, infaunal organisms were not significantly reduced in abundance (Table 2 and Fig. 3). These results for white shrimp agree with the great majority of trends observed by Service et al. (1992) in sediment from North Inlet, South Carolina. The sole exception was *Capitella*. This species of polychaete was significantly reduced, but not highly so, in the South Carolina study, while our results show it not to have been affected by the presence of white shrimp. We cannot account for the difference in this one species but suggest that the low abundance and patchiness of *Capitella* may have confounded the analysis in one or both studies.

Penaeid shrimp are demersal and are generally thought to feed by browsing and digging through surface sediments. Feeding differences between the species of penaeids may be related to their effectiveness in foraging on different prey species. Organisms such as capitellids appear to be simply out of the reach of brown shrimp, while those animals living near the surface may be more accessible prey items. Tubiculous crustaceans at the sediment surface, such as the tanaid *Hargeria rapax* and the amphipod *Ampelisca abdita*, also appear to be more available than free-moving species. During laboratory growth studies (discussed later in this section), free swimming amphipods were provided as food to brown shrimp. The predator had difficulty capturing these amphipods as they swam

quickly around the container. As the 30-d growth experiment continued, both white shrimp and brown shrimp developed a technique in which they gathered the amphipods in the space between the shrimp's walking legs. This more efficient method of capture did not increase their growth rates, however. In nature, tubiculous organisms would be limited in their range of movement and may be more easily located and captured than free-moving organisms.

Differential selection of prey from sediment by brown shrimp may have major implications to infaunal community structure and shrimp production dynamics. Marshes vary widely in species composition of infauna and densities of organisms present, and this variability may be related to physical factors, such as salinity regime. Moreover, the overall abundance of infauna may be misleading as evidence of the quality of a foraging area for brown shrimp. A marsh dominated by deep-dwelling capitellids can have similar infaunal density or biomass as a marsh or another habitat inhabited primarily by spionids. To brown shrimp, however, these areas may be very different. One instance allows little or no access to the prey, while the other offers food in abundance. This may translate into local success or failure of brown shrimp productivity, yet such fine-scale habitat differences are rarely if ever considered.

During the two trial periods for brown shrimp, there were some differences among prey the penaeid could successfully remove from the substrate (Table 1). Notably, for the prey items *Melinna maculata* and chironomids, there was a significant in-
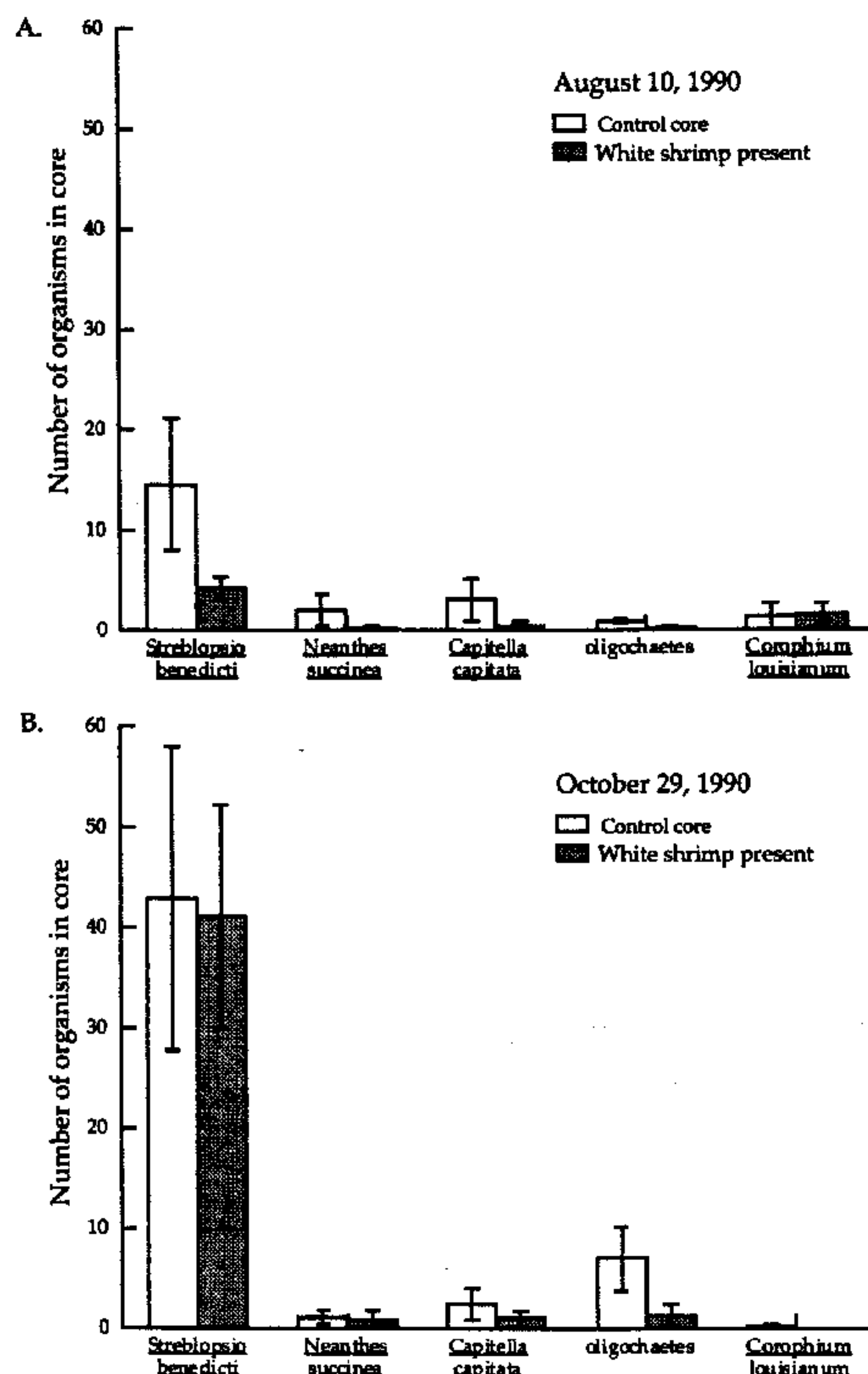
Fig. 3. Depletion of abundant infaunal groups from cores of sediment (area = 78.54 cm²) in which white shrimp were placed for 4 d. Error bars indicate one standard error. (A) Results of the early season experiment beginning August 10, 1990. (B) Results of the late season experiment beginning October 29, 1990.
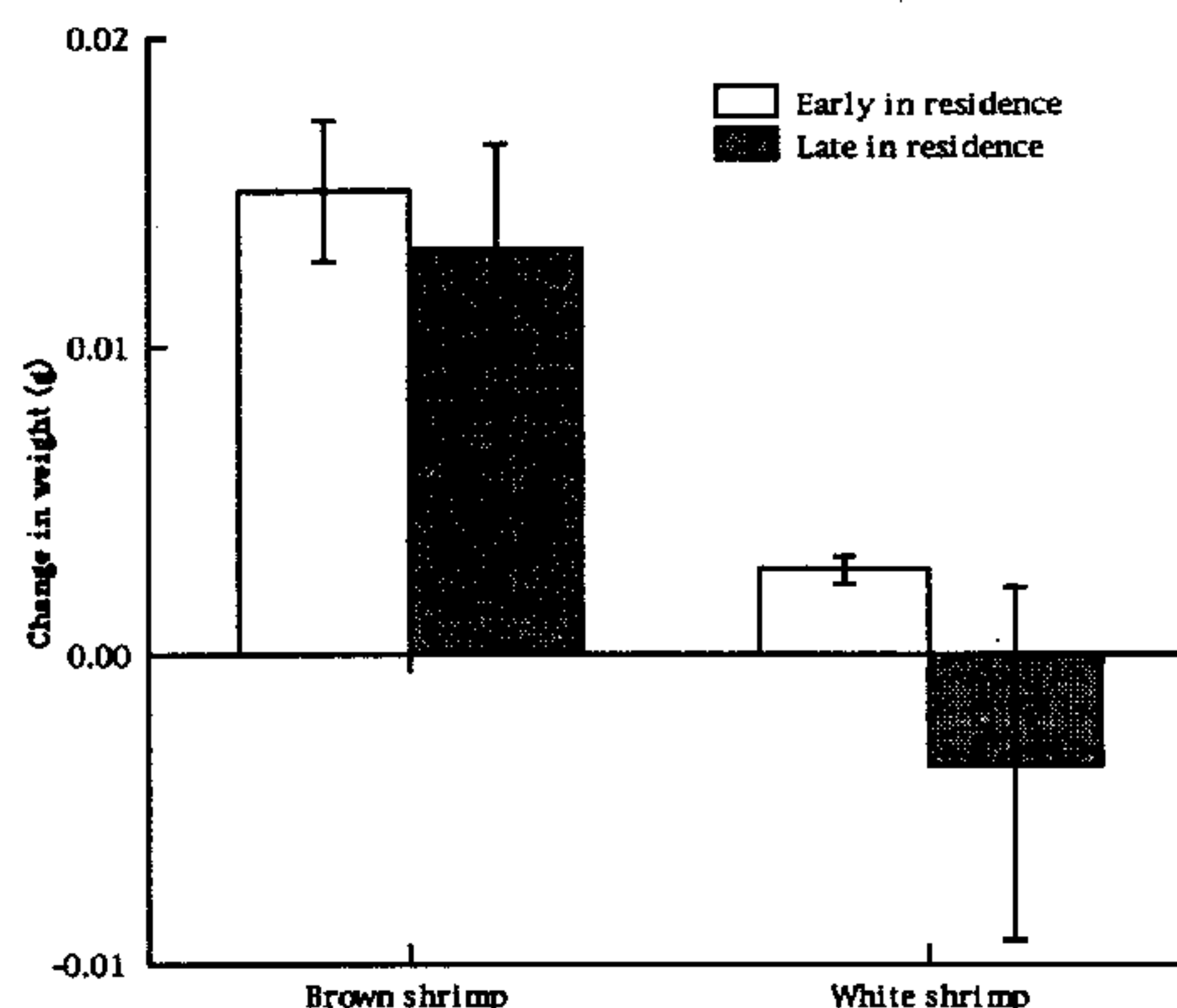

Fig. 4. Weight change for brown and white shrimp during 4-d exposure to cores of natural sediment. Experimental runs occurred early and late during the residence period of each shrimp species. Error bars indicate one standard error.

teraction between the date of the experiment and whether a shrimp was present. The effect of the presence of a brown shrimp was different during the February and May experiments. The cause, most obviously, and perhaps most significantly, was that densities of infauna differed greatly between the two periods. Control cores collected February 27 had an of average 171.4 organisms core⁻¹ (SE = 20.0, core area = 78.54 cm²); representing the period before the annual infaunal decline. By May 5, the mean abundance was 84.7 organisms core⁻¹ (SE = 17.6). The average density of *Melinna maculata* changed from 15.8 per control core (SE = 2.0) in February to less than one per control core (mean = 0.6, SE = 1.0) in May. Chironomids averaged 12.25 organisms core⁻¹ (SE = 1.4485) during the early experiment and 0.3 larvae per control core (SE = 0.2134) during the late experiment. These prey during the later period may have been

simply more difficult to locate if they were present in an individual core at all.

White shrimp did not significantly affect infaunal densities (Table 2 and Fig. 3), despite their highly limited access to alternate food items. Further, after the 4-d exposure to the sediment, white shrimp had gained much less weight than did brown shrimp (Fig. 4). The pattern held true for both early and late season trials of the experiment. Late in their residence period, white shrimp actually lost weight when allowed to feed from marsh surface sediment. One might assume that after a period of time, a starving animal would make use of food resources normally outside its dietary breadth. White shrimp may have consumed something in the core not measured (benthic algae?). It seems reasonable to suggest, as well, that this penaeid may be poorly equipped to locate and capture infauna. Both hypotheses correspond with distribution and temporal patterns known for white

TABLE 3. Analysis of variance of survival of brown and white shrimp fed experimental diets. Data were log transformed because of heterogeneity of variances.

Dependent variable: days survived (log transformed)

Source	d.f.	Sum of Squares	Mean Square	F-Value	p-Value
Model	11	26.8944	2.4449	20.18	0.0001
Error	268	32.4645	0.1211		
Corrected total	279	59.3589			

Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Species	1	4.2683	4.2682	35.24	0.0001
Diet	5	21.5620	4.3124	35.6	0.0001
Species × diet	5	2.7512	0.5503	4.54	0.0005

TABLE 4. Contrasts performed on shrimp survival data within and between shrimp species fed various diets, including polychaete, amphipod, polychaete + *Skeletonema*, and amphipod + *Skeletonema* diets. An asterisk denotes significant differences at the $\alpha = 0.05$ level.

| Contrast	F-Value	p-Value
Brown shrimp versus white shrimp		
Overall	35.24	*0.0001
Animal + plant diets	16.94	*0.0001
Animal material only diets	14.96	*0.0001
Polychaete-based diets	2.42	0.1211
Amphipod-based diets	42.13	*0.0001
Brown shrimp		
Polychaete based diets versus all others	2.50	0.1150
Control (starved) versus all others	78.57	*0.0001
Animal + plant diets versus all others	17.39	*0.0001
Polychaete versus polychaete + *Skeletonema*	0.14	0.7073
Amphipod versus amphipod + *Skeletonema*	0.78	0.3776
Skeletonema versus animal + plant	29.38	*0.0001
White shrimp		
Polychaete based diets versus all others	22.02	*0.0001
Control (starved) versus all others	34.46	*0.0001
Animal + plant diets versus all others	5.65	*0.0182
Polychaete versus polychaete + *Skeletonema*	15.78	*0.0001
Amphipod versus amphipod + *Skeletonema*	0.02	0.8969
Skeletonema versus animal + plant	14.78	*0.0002
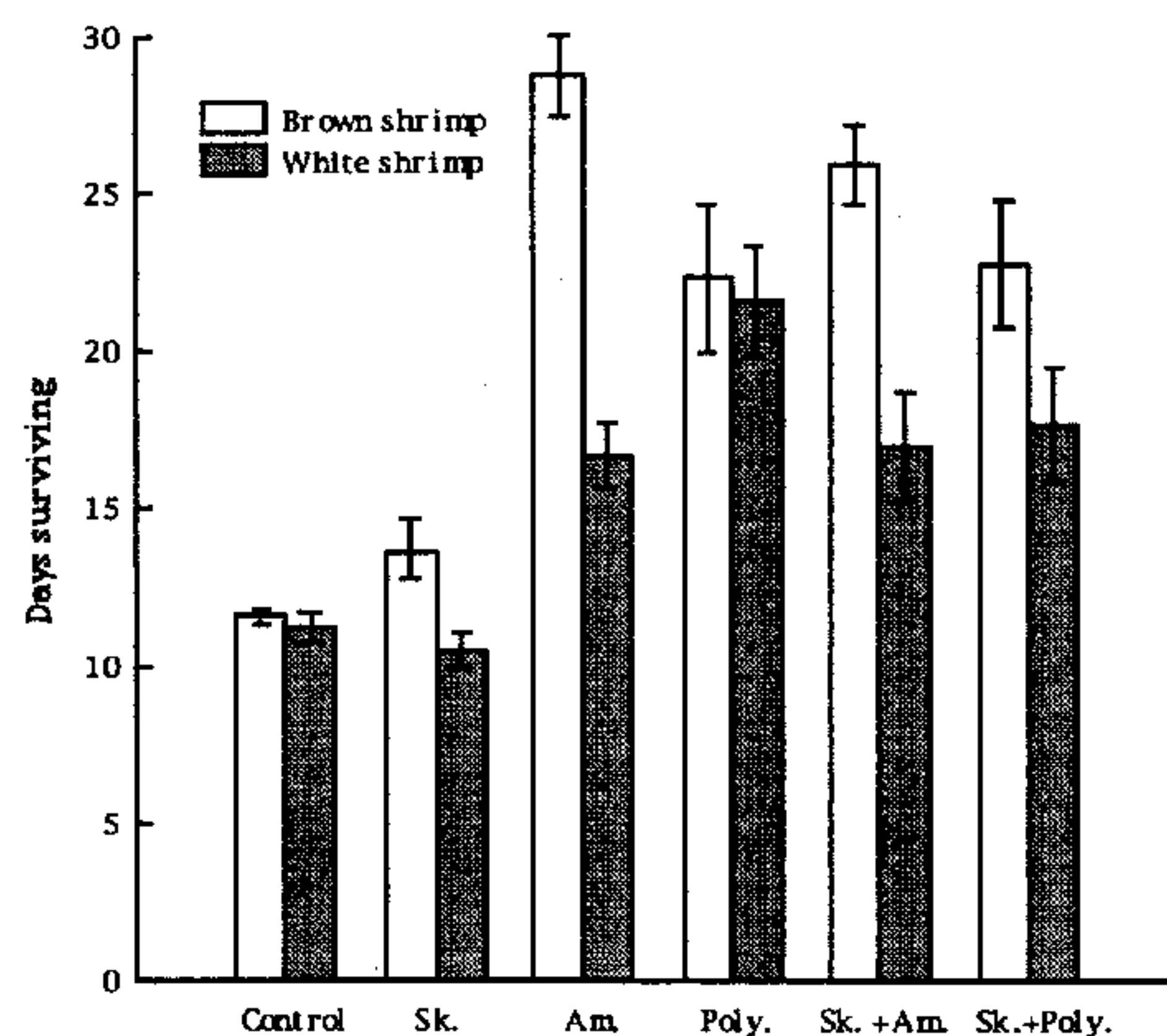
Fig. 5. Number of days brown shrimp and white shrimp survived in experimental containers when fed the following treatment diets: Control = starved, Sk. = *Skeletonema*, Am. = amphipods, Poly. = polychaetes, Sk. + Am. = *Skeletonema* and amphipods, Sk. + poly. = *Skeletonema* and polychaetes. Error bars indicate one standard error.

shrimp, although it is unlikely that much of their preferred food was available as they gained little or no weight.

Brown shrimp survived longer than did white shrimp overall, and lived longer when fed animal material alone or in combination with *Skeletonema* (Tables 3 and 4, and Fig. 5). Both species of penaeids survived longer on diets that incorporated animal material over algae alone (Table 4). Brown shrimp appeared to have higher survival rates, but grew less, when fed amphipods versus polychaetes. Survival, however, may not be appropriate for comparing the relative value of the diets. Polychaete worms were more likely to degrade the quality of

TABLE 5. Repeated measures analysis of variance (ANOVA) of incremental growth of brown and white shrimp fed experimental diets. Data were log transformed because of heterogeneity of variances. The analysis included 20 d of the growth study. An asterisk indicates significance at the $\alpha = 0.05$ level.

Dependent variable: weight change in 5 d (log transformed)
Tests of hypotheses for between-subject effects

Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Species	1	0.01938	0.0194	192.29	*0.0001
Diet	3	0.0379	0.0126	125.49	*0.0001
Species × diet	3	0.0184	0.0061	60.97	*0.0001
Error	73	0.0074	0.0001		

Tests of hypotheses for within-subject effects

Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Time	3	0.0040	0.0013	6.94	*0.0002
Time × species	3	0.000017	0.000006	0.03	0.9934
Time × diet	9	0.0047	0.0005	2.71	*0.0051
Time × species × diet	9	0.0023	0.0003	1.34	0.2198
Error	219	0.0420	0.0002		

TABLE 6. Repeated measures analysis of variance (ANOVA) of incremental growth of brown and white shrimp fed experimental diets. Data were log transformed because of heterogeneity of variances. The analysis included 20 d of the growth study. An asterisk indicates significance at the $\alpha = 0.05$ level.

Dependent variable: weight change in 5 d (log transformed)

Day 0 to Day 5

F-Value = 13.68   p-Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Species	1	0.0047	0.0047	26.68	*0.0001
Diet	3	0.0054	0.0018	10.26	*0.0001
Species × diet	3	0.0046	0.0015	8.61	*0.0001

Day 5 to Day 10

F-Value = 34.17   p-Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Species	1	0.0053	0.0053	66.62	*0.0001
Diet	3	0.0089	0.0030	37.58	*0.0001
Species × diet	3	0.0036	0.0012	15.36	*0.0001

Day 10 to Day 15

F-Value = 13.39   p-Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Species	1	0.0045	0.0045	23.39	*0.0001
Diet	3	0.0088	0.0029	15.3	*0.0001
Species × diet	3	0.0026	0.0009	4.44	*0.0064

Day 15 to Day 20

F-Value = 26.84   p-Value = 0.0001*

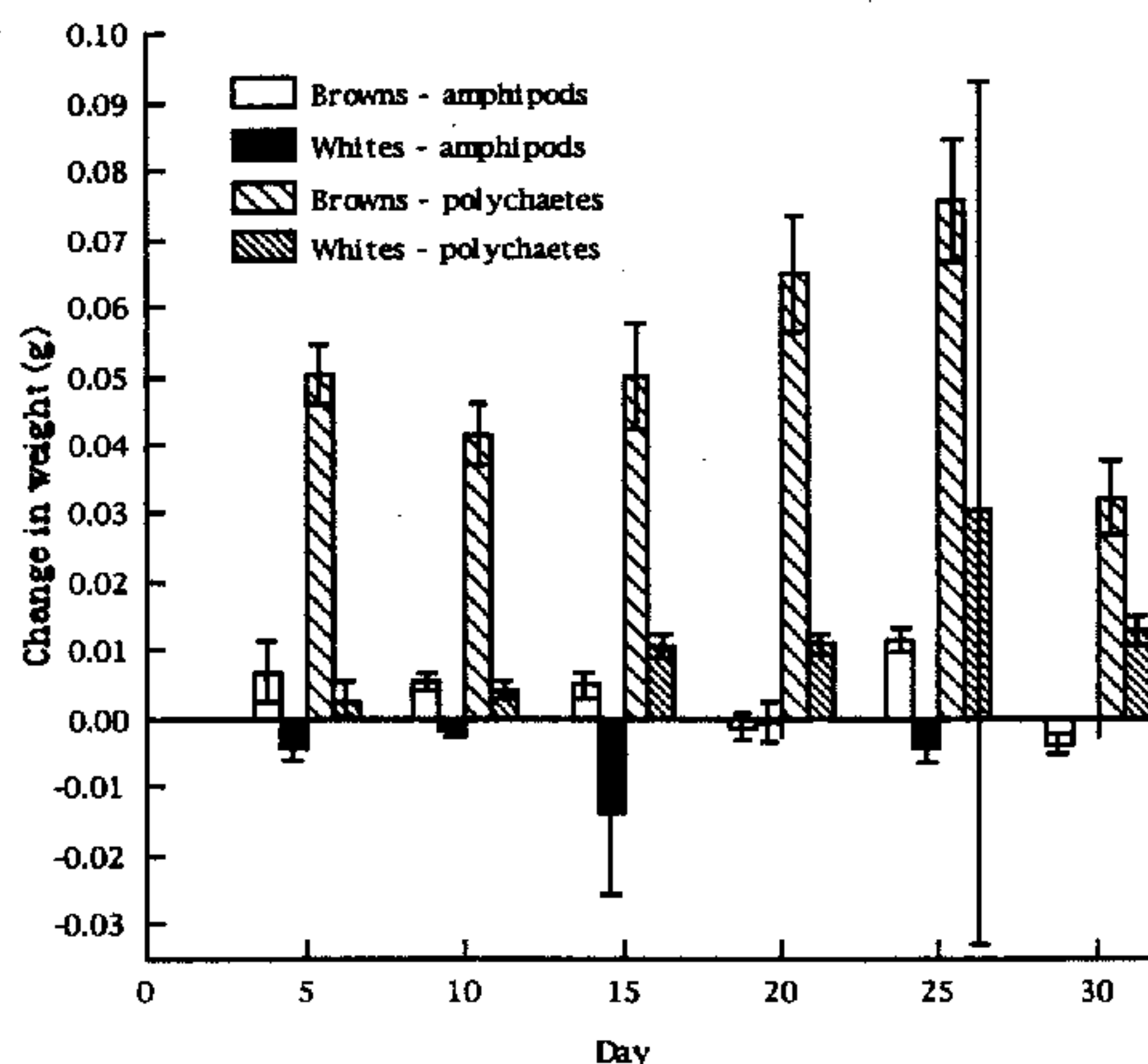| Source	d.f.	Type III S.S.	Mean Square	F-Value	p-Value
Species	1	0.0049	0.0049	21.58	*0.0001
Diet	3	0.0195	0.0065	28.37	*0.0001
Species × diet	3	0.0100	0.0033	14.55	*0.0001

Fig. 6. Change in weight for brown shrimp and white shrimp fed amphipod and polychaete diets during 5-d periods over 30 d. Error bars indicate one standard error.

seawater in the treatment beakers than were amphipods, possibly impacting the shrimp. In addition, shrimp fed polychaete-based diets were much more active than those in other treatments. They were more likely to die accidentally by jumping and adhering to the wall of the beaker above the water line or leaving the beaker entirely, despite the cover provided. To compare the relative quality of the faunal diets, growth of the shrimp was the best measure used.

TABLE 7. Contrasts associated with ANOVA procedures performed on shrimp incremental growth data within and between species of shrimp including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets. The numbers refer to the p-value of the contrast and an asterisk denotes significant differences at the $\alpha = 0.05$ level.

| Contrast	Period of Time			
	Days 0–5	Days 5–10	Days 10–15	Days 15–20
Brown shrimp versus white shrimp				
Overall	*0.0001	*0.0001	*0.0001	*0.0001
Animal + plant diets	0.0987	*0.0001	*0.0115	0.0548
Polychaete-based diets	*0.0001	*0.0001	*0.0001	*0.0001
Amphipod-based diets	0.4164	*0.0460	0.2823	0.4925
Animal material only diets	*0.0001	*0.0001	*0.0001	*0.0001
Brown shrimp				
Polychaete versus polychaete + Skeletonema	*0.0444	*0.0001	0.2343	0.1513
Amphipod versus amphipod + Skeletonema	0.3785	*0.0066	0.9252	0.6513
Amphipod versus polychaete	*0.0001	*0.0001	*0.0001	*0.0001
Amphipod + Skeletonema versus polychaete + Skeletonema	*0.0001	*0.0001	*0.0001	*0.0001
White shrimp				
Polychaete versus polychaete + Skeletonema	0.8527	0.4409	0.6277	0.4471
Amphipod versus amphipod + Skeletonema	*0.0220	*0.0189	0.5364	0.3425
Amphipod versus polychaete	0.0690	0.5477	*0.0292	0.0832
Amphipod + Skeletonema versus polychaete + Skeletonema	0.3265	0.0951	0.6909	0.3843
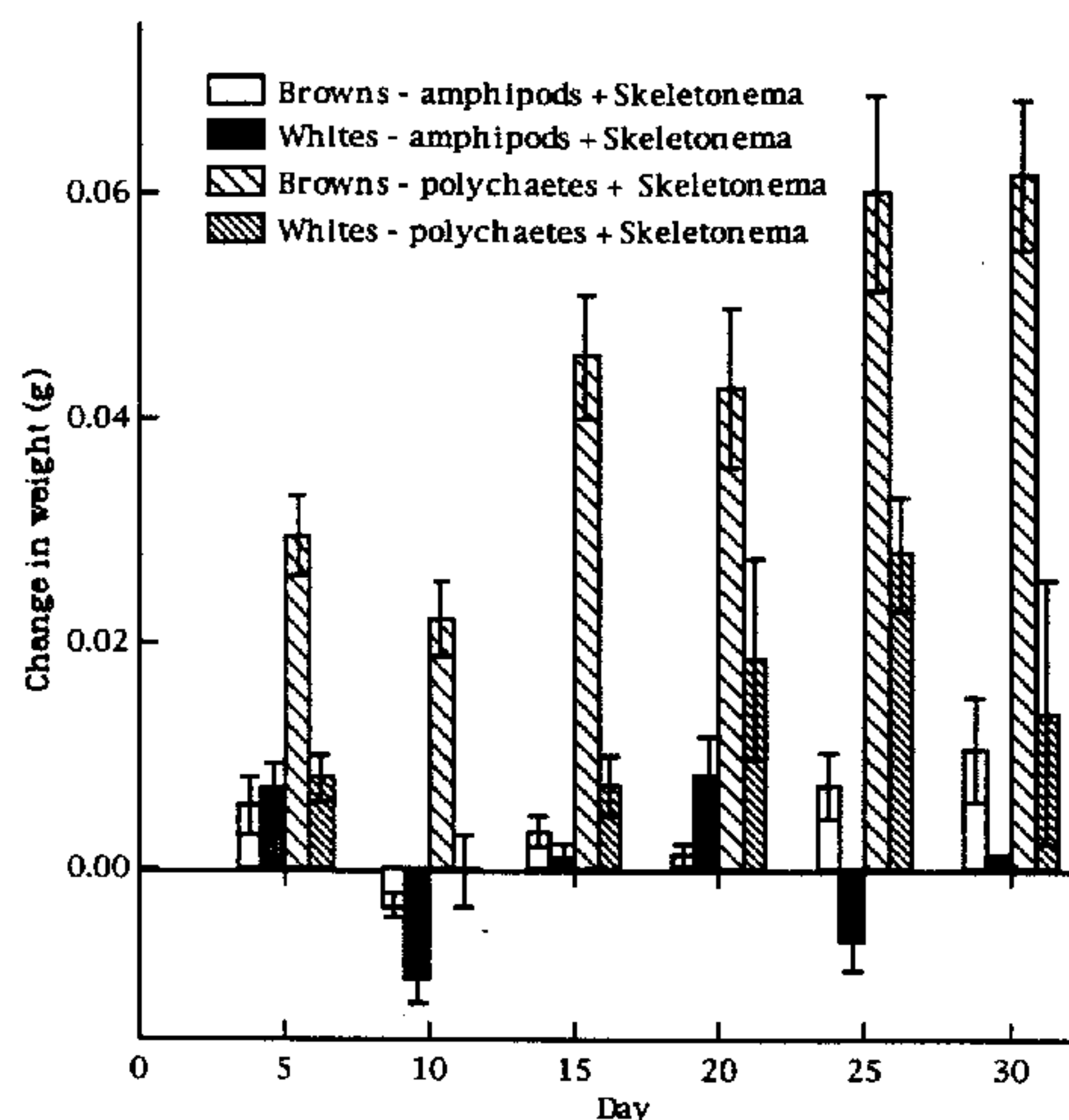
Fig. 7.   A comparison of weight change for brown shrimp and white shrimp fed combination animal and plant material diets during 5-d periods over 30 d. Error bars indicate one standard error.

Brown shrimp and white shrimp differed in their growth response to the diets, and the magnitude of that difference increased over time (Tables 5 and 6, and Figs. 6 and 7). Brown shrimp consistently grew at a greater rate on the diets provided than did white shrimp. This is contrary to evidence from the field and laboratory that suggests white shrimp grow more quickly than do brown shrimp
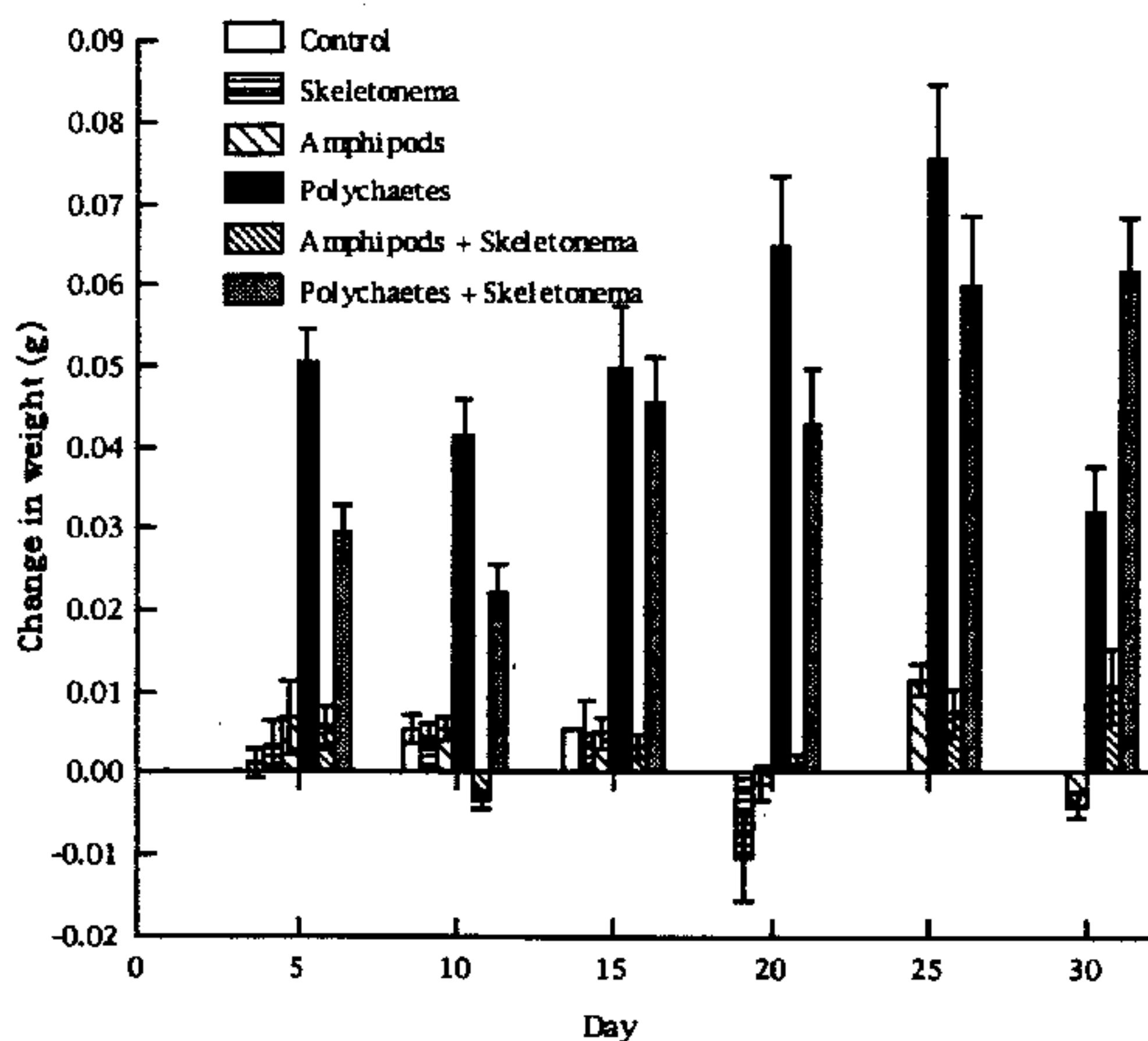
Fig. 8.   Change in weight over 5-d periods for brown shrimp fed experimental diets of salt marsh infaunal organisms and the diatom *Skeletonema*. Error bars indicate one standard error.
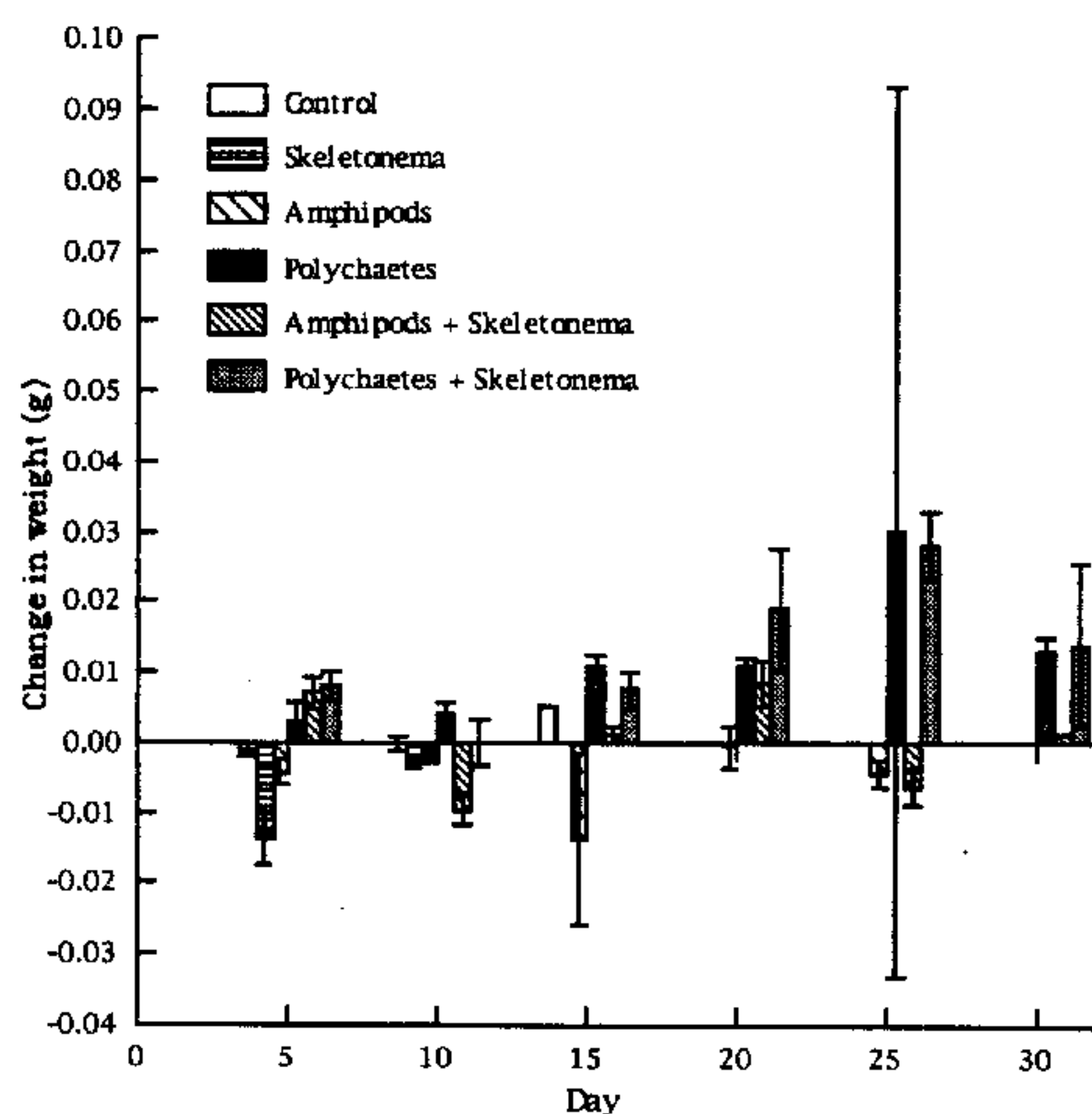

Fig. 9.   Change in weight over 5-d periods for white shrimp fed experimental diets of salt marsh infaunal organisms. Error bars indicate one standard error.

(Johnson and Fielding 1956; Wheeler 1968; Knudsen et al. 1977). This discrepancy may be related to the restricted diets provided during this study. Penaeids feeding in cages in the field have access to a wider variety of food and are more likely to encounter their preferred food source. For the white shrimp, the diets provided appear to have been lacking in some way as maximum growth rates observed in nature were not achieved.

Polychaete-based diets consistently produced more growth in brown shrimp than in white shrimp (Table 7). Amphipods were a poor diet for
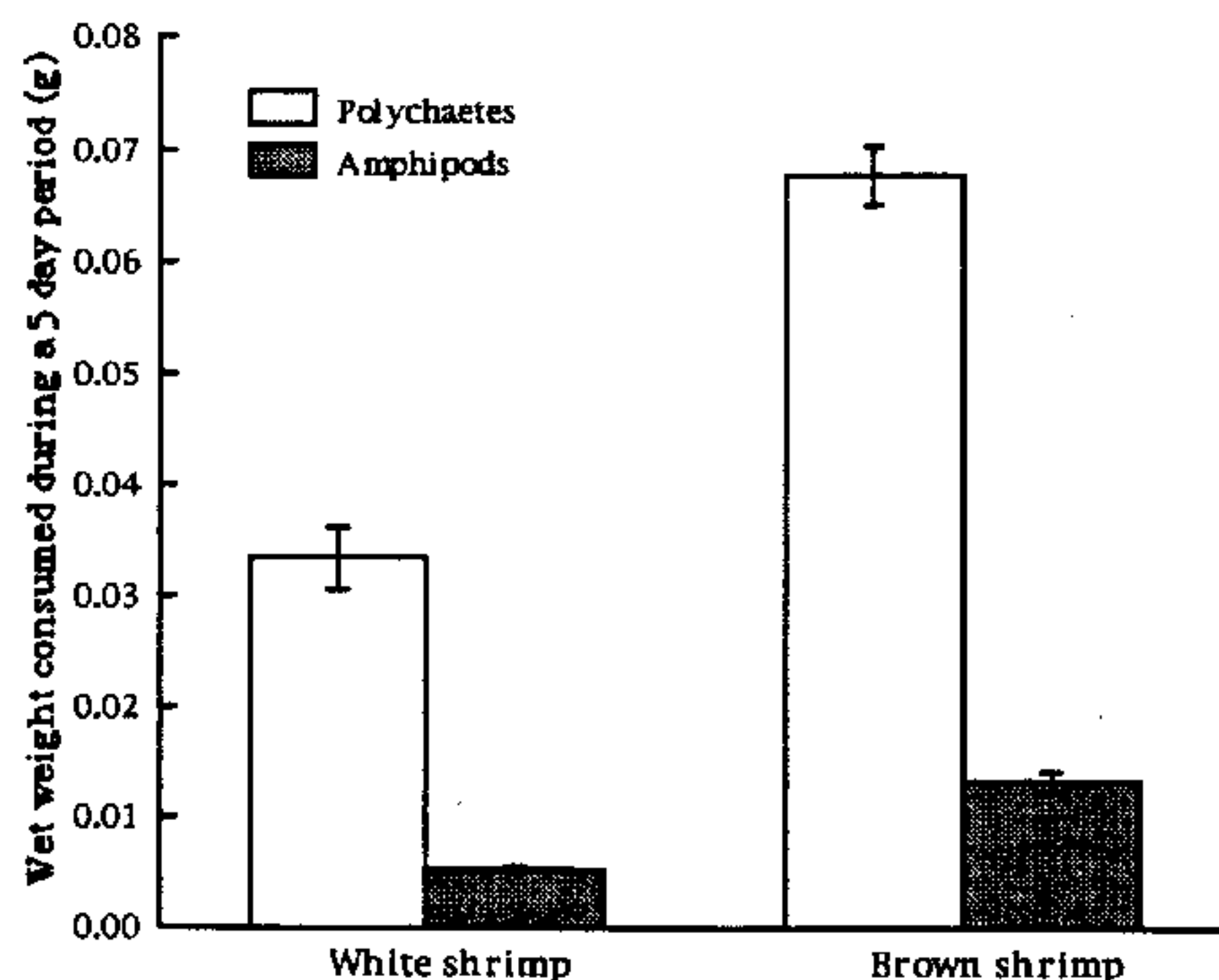

Fig. 10.   Average consumption of prey items by white and brown shrimp over a 5-d period. Values are wet weights and are from dietary treatments that included the diatom *Skeletonema*. Error bars indicate one standard error.

both species, producing little growth regardless of whether algae were present (Table 7, and Figs. 8 and 9). The consumption of amphipods by brown shrimp under laboratory conditions has been taken to indicate that the penaeid is an important predator of these animals in the field (Nelson 1979). While the shrimp may be potentially significant in the structuring of the infaunal population, amphipods would seem of secondary importance in a penaeid's diet. Brown shrimp consistently consumed more of the fauna provided in the combination treatments (Fig. 10), although neither species ate as many amphipods by weight as they did polychaetes. White shrimp may have utilized the diatoms present.

Incremental growth values in the current research fall well below those reported for brown and white shrimp fed brine shrimp (*Artemia*) and *Skeletonema* under a similar experimental system (McTigue and Zimmerman 1991). This difference can be viewed in several ways. First, *Artemia* nauplii (used in McTigue and Zimmerman 1991) during the first few days of life are nutrient-rich, still harboring yolk reserves. Second, they may resist capture to a lesser degree than polychaetes and amphipods, resulting in less energy expenditure by the predator. The difference in growth rates for brown shrimp may be significant, but it in no way approaches the contrast seen in white shrimp. In the current research, between days 20 and 25 white shrimp added an average of 0.0278 g (SE = 0.0050) when fed polychaetes and *Skeletonema*. The change in weight resulting from an *Artemia* and *Skeletonema* diet between days 20 and 24 was approximately 0.17 g. This suggests that because of some nutritional value or behavioral advantage, brine shrimp as compared with infauna may approximate more closely the white shrimp's natural, but unknown, faunal food source.

Given that infauna are unlikely to be a significant faunal element in the diet of juvenile white shrimp, the penaeid must be utilizing another reasonably accessible group of prey items. A potential alternate faunal food source for juvenile white shrimp may be estuarine mysids. These small, free-swimming crustaceans are found in the water column and have been identified in the proventriculus of several species of penaeids (Chong and Sasekumar 1981; Suthers 1984). *Penaeus plebejus*, in a sample from Sydney Harbor, Australia, had guts filled almost entirely with the mysid *Rhopalophthalmus dakini* (Suthers 1984). While they have not been reported from the guts of white shrimp, mysids are very common in marshes and adjacent open bottom areas, including the areas sampled in this study. Their absence from white shrimp guts may be due to trituration by the penaeid's gastric

mill. Further, white shrimp held in aquaria often can be seen hovering in the water column (Z. Zein-Eldin personal communication) and may be capturing food there. Other potential food sources could include various forms of zooplankton, such as copepods, although this is simply speculation. These two species of shrimp, long considered to be rather similar, may have significantly different trophic roles.

Marshes are considered important nurseries for penaeid populations. These areas can vary in many respects, including accessibility of the marsh surface and presence of accessible prey. While many areas are classified as estuarine marshes, they may be lacking in the basic requirements for success of penaeid populations. An understanding of the basic life-history requirements of a particular shrimp species may help to draw a more complete picture of their role in a particular region. Salt marshes along the southern Atlantic coast and the northern Gulf of Mexico tend to be dominated by similar plants. They can differ greatly as habitats, however, in terms of marsh geomorphology, inundation periodicity, and tidal regime. Such differences may have a significant role in determining marsh utilization patterns by nekton, such as both brown shrimp and white shrimp (Rozas 1993; Rozas and Reed 1993). Wenner and Beatty (1993) compared shrimp densities and catch statistics from salt marshes and the nearshore waters of South Carolina with those published for Texas by Zimmerman and others. They found that although South Carolina had much more extensive marshes, penaeids were found in greater densities in Texas waters. This held true for the in situ density measurements of shrimp in marshes as well as for the commercial landings. It was suggested that the more solid stands of vegetation in the east coast marshes with 1.5 m tides and lower duration of inundation offered less access to the marsh surface for penaeids than those in the Gulf. The result may be higher mortality rates due to less marsh refugia and increased predation pressure.

We postulate that predation is not the only mechanism influencing the success of shrimp populations in marsh nursery areas. Limited access to the marsh surface would also affect availability of potential prey. A marsh with great tidal exchange and little edge area would offer less actual foraging time on the infauna-rich marsh surface. Instead of residing on the marsh in stands of high water as seen in the northwestern Gulf, the shrimp in South Carolina marshes would spend significant amounts of time migrating back and forth with ebb and flood waters. Further, for several hours each day penaeids would be limited to tidal creeks with high levels of competition for limited resources, as well

as increased predation rates. Wenner and Beatty (1993) also indicated that the numerically dominant penaeid in South Carolina marshes is the white shrimp. In the marshes of Galveston Bay, brown shrimp are more common than either white or pink shrimp (*Penaeus duorarum*). We believe that the difference in dominant species may be related to food resources available in the respective areas. In South Carolina, the dominant penaeid is the one that does not significantly select for the marsh surface and may make little use of infaunal resources. As a result, white shrimp can prosper in an area with limited marsh access. In Texas, brown shrimp, which appear to be infaunal feeders, are dominant in marshes that allow ample access to areas densely populated by their potential prey. Predation may play a role in overall population levels, but the dominance of one species over the other correlates well with what is known of their trophic dynamics.

In Atlantic estuaries, white shrimp are thought to first move toward the upper reaches of a system and gradually migrate back to ocean waters as they approach adulthood (Williams 1984; Kneib 1995). In marshes adjacent to Sapelo Island, Georgia, this large-scale movement of white shrimp through the estuarine system seems to be inversely related to the pattern of infaunal abundance (Kneib 1995). When large concentrations of white shrimp were found in a marsh, infaunal densities tended to be low. Conversely, when white shrimp were present in low numbers, the infaunal population in that marsh appeared to be high. Feeding by the shrimp was suggested as a potential factor in the depression of infaunal abundances. This potential causal relationship conflicts with the results of the current study as well as those of Service et al. (1992). White shrimp did not deplete the total number of macroinfauna in either study, nor did they impact the abundances of individual species of infauna, although Service et al. (1992) report a decrease in *Capitella*. It seems likely that a factor other than white shrimp feeding may be determining the trends in infaunal abundance.

The results reported here for shrimp predation upon amphipods are in contrast to those discussed by Nelson (1979) for pinfish (*Lagodon rhomboides*) and grass shrimp (*Palaemonetes vulgaris*) feeding in seagrass beds. Our research indicates that, in salt marshes, tubiculous amphipods are at significantly higher risk than free-swimming species of being preyed upon by brown shrimp. In seagrass beds, however, amphipod tubes offered a protective advantage to their residents over free-living organisms. Nelson (1979) felt that predation was a primary force in determining the abundance and diversity of amphipods in seagrass beds. Contrasts in our results may be related to both differences in the predators and the habitats considered. Brown shrimp walk along surfaces, probing and handling the substrate. They may have a higher success rate at locating cryptic prey than would a more nektonic animal, such as a pinfish. Grass shrimp may have difficulty in penetrating the substrate to any great degree, as may be true for white shrimp. While *Palaemonetes* are known to consume meiofauna (Bell and Coull 1980), removing a relatively large, active amphipod from its tube may be beyond the ability of the grass shrimp. Both salt marshes and seagrass beds are, of course, vegetated, but the variance in plant morphology may necessitate different foraging strategies.

Variation in the effects of predation can be significant in the structuring of an infaunal population. In seagrass beds, Leber (1985) studied the effects of feeding by pink shrimp (*Penaeus duorarum*) and other predators on amphipod communities. He found that predation coupled with microhabitat availability resulted in varying levels of pressure being exerted on the different species of amphipods. Similarly, Nelson and Capone (1990) demonstrated that predators feeding in seagrass beds, including pink shrimp, selectively remove certain groups of polychaetes over others and may play a significant role in structuring the infaunal assemblage within a seagrass habitat. This pattern may be replicated in both polychaetes and amphipods in salt marshes, although the species impacted vary. Certain groups, such as surface-dwelling polychaetes and tubiculous amphipods, may be affected more greatly by shrimp predation in a salt marsh system. Selective removal of these forms could both impact abundance and diversity of the community. Further, there appears to be unequal trophic contributions by infaunal groups. The presence of certain amphipods or polychaetes may play a greater role in local predator productivity than others.

Brown shrimp can be significant predators of infauna, but the degree of significance appears to change with the type of prey considered. Although not discussed here, there is likely to be a seasonal and perhaps a habitat component to the significance as well (Young et al. 1976; Young and Young 1978). Further, brown shrimp are not the only predators of infauna in estuarine areas. During their estuarine residence period, however, they are significantly attracted to the marsh surface with its abundance of polychaetes. Overall, predation by organisms such as brown shrimp may define infaunal communities by selectively impacting certain groups, in this case superficial dwelling polychaetes and tubiculous amphipods.

Brown shrimp and white shrimp belong to dis-

tinctly different subgroups within the penaeids: grooved versus nongrooved shrimp (differentiated by the presence or absence of adrostral sulci, grooves to either side of postrostral carina or ridge). Dietary differences observed between the two species may reflect long-term patterns indicative of their groups. Insufficient information exists in the literature to test this theory. While no evidence is available to confirm or refute the idea, the divergence between the species may also have resulted from competition. It would be impossible to tell, however, which aspect of their life history was initially involved.

Conclusion

Brown shrimp and white shrimp are physically similar animals that appear to have very different ecological roles in salt marshes. These differences are manifested in several aspects in their respective life cycles.

Brown shrimp are among the earliest of spring immigrants into estuaries. Their distribution between vegetated and nonvegetated areas directly reflects the relative abundances of infauna in those two habitats. When populations of worms are great in both the marsh and open water sediments, the shrimp are equally distributed between the two areas. As open water densities of prey decrease, brown shrimp tend to concentrate on the marsh surface. While described as an omnivore, the brown shrimp relies most heavily on the faunal element of its diet. Previous research has indicated that at least some plant material appears to be necessary, though, to optimize growth rates. Brown shrimp effectively remove infauna from natural sediments and grow when fed polychaetes (and amphipods to a lesser extent) under laboratory conditions.

White shrimp appear in marshes in late spring or early summer, when potential infaunal food sources previously available may already be depleted. Once in estuarine areas, these shrimp are very patchy in distribution and are often found equally in vegetated and nonvegetated areas. While they, too, are omnivorous, the white shrimp may rely less on the faunal element of its diet than does the brown shrimp. Moreover, the dominant animal component of the white shrimp's diet has yet to be determined. They do not remove infauna from natural sediment to any significant degree, nor do they grow well when fed polychaetes or amphipods in the laboratory. White shrimp do not have a clear linkage to infaunal populations as do brown shrimp. Given that they seem to spend more time swimming than do brown shrimp, white shrimp may utilize more planktonic resources, such as mysids.

Specific feeding requirements for these shrimp may impact their success both locally and between regions. On a small scale, the community structure of an individual salt marsh may affect the penaeid's ability to forage in the area. For brown shrimp, if the infaunal population is dominated by deep-burrowing polychaetes as opposed to surface-dwelling species, there may be insufficient food resources to support a large penaeid population. White shrimp, too, probably have an optimum faunal group that may restrict their effective utilization of an area. At present, this group is not known.

Shrimp feeding requirements may, in part, help to explain differences between regions. White shrimp are the numerically dominant species in the marshes of South Carolina. In Texas salt marshes, by contrast, brown shrimp outnumber other penaeid species, including white shrimp. Further, Texas has higher overall densities of shrimp than does South Carolina. The two regions differ greatly in the accessibility of marsh habitat, both through inundation patterns and degree of reticulation. South Carolina may have large amounts of marsh area, but the 1.5 m tidal height and relatively solid stands of cordgrass allow shrimp only brief access to vegetated areas. It has been suggested that predation is responsible for the density differences in the two habitats. This may not be the complete answer. South Carolina not only has fewer shrimp per unit area than Texas, but a different species dominates. These patterns may be a result of feeding differences as well as differential predation pressure. In South Carolina, with restricted marsh access, white shrimp occur in greater densities than other penaeids. In Texas, patchy marshes and an approximately 30 cm tidal height allow mobile species greater access to vegetated areas. Brown shrimp, the species more reliant on infauna, is dominant in these marshes. While a variety of factors may be involved, it is tempting to speculate that feeding requirements play a role in this large-scale distributional difference.

Brown shrimp and white shrimp superficially appear to be quite similar animals. Closer examination through this and other research has shown that the two species diverge on a series of interrelated points.

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